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THE SKELETON OF THE LOWER CARBONIFEROUS LABYRINTHODONT *PHOLIDOGASTER PISCIFORMIS*

By Alfred Sherwood Romer

WITH ONE PLATE

No. 6 — *The Skeleton of the Lower Carboniferous Labyrinthodont* Pholidogaster pisciformis

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INTRODUCTION

Although the ancient labyrinthodont amphibians are of over-whelming importance in the story of tetrapod evolution, our knowledge of their early evolution and radiation is still exceedingly fragmentary. On the one hand, we are fortunate in having materials (as yet not fully described) from the late Devonian of East Greenland (Säve-Söderbergh, 1932; Jarvik, 1952, 1955) which illustrate a very early phase of amphibian history; on the other, we have a very considerable knowledge of Permian and Triassic labyrinthodonts. But most of the crucial stages in labyrinthodont evolution obviously occurred during the Carboniferous, and here our knowledge is distressingly incomplete. A fair amount of material is known from the later Carboniferous — the Pennsylvanian — but is as yet far from adequately described. Poorer still is the situation as regards the earlier — Mississippian — stage of the Carboniferous. A very limited amount of North American material of this age from West Virginia is now known and under description by Hotton and the writer. Otherwise, as reviewed by Watson (1929; cf. Panchen and Walker, 1960, pp. 327-328), Lower Carboniferous labyrinthodonts are known only from a very few specimens from Scotland, and these are mainly of a fragmentary nature.

In consequence, the type of *Pholidogaster pisciformis* Huxley is of unique importance as the only articulated skeleton of a Lower Carboniferous labyrinthodont described up to the present time. As noted by Huxley (1862), the specimen, discovered in the Gilmerton Ironstone of the Edinburgh coalfield over a century ago, was originally acquired by Sir Philip Egerton and the Earl of Enniskillen, "but as, on mature consideration, it appeared to them not to be a fish, it was handed over to the British Museum." Huxley described it briefly. Watson, in his 1929 review of Carboniferous labyrinthodonts, gave an account of such anatomical features as could then be made out. Recently Mr. A. E. Rixon has further prepared the specimen, revealing a considerable amount of new anatomical data, particularly as regards the trunk vertebrae, thus rendering further description advisable.

I wish to thank Keeper Errol I. White for the privilege of studying this important specimen. I am grateful for the friendly and helpful reception given me at the British Museum during the course of this work, not only by Dr. White but by other members of the staff, particularly Dr. W. E. Swinton and Mr. Barney Newman. And I am, of course, particularly indebted to Mr. Rixon for undertaking the preparation of this difficult material.

The specimen comes from the Gilmerton Ironstone of Gilmerton, in the Midlothian Coalfield of the Edinburgh region. As noted by Panchen and Walker (1960, p. 328), the horizon is close to the base of the Carboniferous Limestone Series. The only amphibians of greater age, apart from the ichthyostegids of East Greenland, are a few small lepospondyls and the unique *Otocratia* skull from the underlying Oil Shale Group of the Calciferous Sandstone Series of the Scottish lowlands. The amphibian remains now under study from West Virginia are from horizons near the summit of the Mississippian, and hence later in time of deposition than Gilmerton.

DESCRIPTION

Huxley's original figure shows the general character of the specimen (his pl. XI, fig. 3), although the artist has taken certain liberties with it (circular objects which he supplied in the head region suggest orbits, but the view here is ventral; the vertebral column which he pictures in the trunk region was drawn largely from his imagination, not from the material). A more accurate representation is given in my Plate I, A (in which, however, the squamation is omitted); details are shown in Figures 1 and 2. The skeleton (BMNH No. 30534) is preserved on a series of small slabs which for the most part fit together without apparent gaps; almost the complete animal was present in articulated fashion. Skull, jaws and trunk are seen in ventral view; the tail is seen from the left side. Decomposition appears to have set in to some degree before burial, so that most of the belly wall and its armor of scales, broadly visible the length of the trunk, lies mainly to the (morphological) right side of the column. The total length as preserved is 117 cm. As Huxley notes, the specimen was in "a very indifferent state of preservation," and its natural condition was not improved by preparation, a century ago, of a rather crude nature. When studied by Watson much of the structure of the

tail and pelvic area was visible, as well as the surface of the
under side of the head and shoulder region. Mr. Rixon's further
preparation dealt mainly with the trunk vertebrae and part
of the dorsal surface of the head. Since the skull is poorly pre-
served and little can be told of the anterior part of the body,
I shall reverse the customary sequence in description, and
begin with the axial skeleton of the tail, leaving skull and jaws
to the last.

Tail. Nearly the complete tail is present. Parts of three
vertebrae are missing in the gap between the block containing
the pelvic region and those containing the rest of the tail, and
another somewhat farther back where a surface chip is missing
from the block. Allowing for these missing areas, thirty-one
caudals are present back of the position of the presumed sacral
vertebra. The tail is comparable in length with that seen in
ichthyostegids, on the one hand, and various temnospondyls,
on the other, but is shorter than that seen in many primitive
reptiles and in the embolomere *Archeria.*

It would appear that when the specimen was discovered
the slab split in such fashion that the tail was immediately
exposed. However, the split ran for the most part through the
substance of the vertebrae, so that surfaces of the elements
are but poorly seen. The net result is that interpretation of
the material is difficult. In the figures, I have endeavored to
outline the structures exactly as preserved, resisting the tempta-
tion to give subjective restoration of obscure areas.

As a result of the poor condition of the material, it is diffi-
cult to tell which side of the tail we are looking at. On one
margin are seen wedge-shaped neural arches from which neural
spines slant diagonally backward; on the opposite margin are
almost identically shaped intercentra and haemal spines. But
which is which? Watson believed that the view was from the
left, so that, for example, in my Plate I, figure A the neural
arches and spines lie along the lower margin. My own conclu-
sions, based on more evidence than was available to Watson,
were at first that the view was from the opposite, right, side,
basing my belief on the fact that the posterior trunk vertebrae
are seen somewhat to the right of a direct ventral view, and that,
hence, one would expect a continuation of this twist on toward
the tail. But the left half of the pelvic girdle lies uppermost
and, most especially, the structure of the caudal vertebral ele-
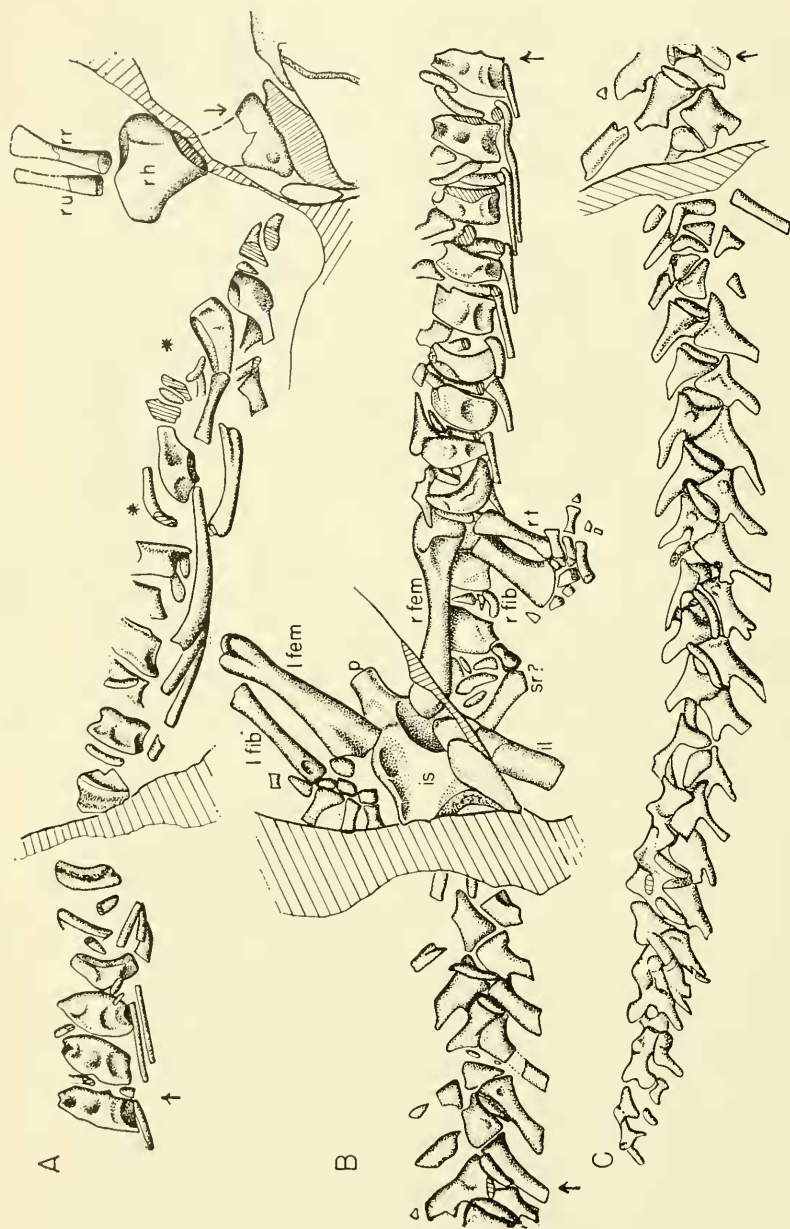ments is reasonably interpretable only from the Watson point

Figure 1. Successive segments of postcranial skeleton as preserved. Arrows are at identical points in successive drawings. A, shoulder to middorsal region; B, posterior dorsal, sacral and proximal caudal region; C, remainder of tail, × ½. Stars indicate position of centra concealed by matrix. Abbreviations: il, ilium; is, ischium; l fem, left femur; l fib, left fibula; p, pubis; r fem, right femur; r fib, right fibula; r h, right humerus; r r, right radius; r t, right tibia; r u, right ulna; sr, sacral rib.

of view. Obviously, body and tail were sharply twisted on one another at the pelvic region.

The vertebral structure of the tail, as Watson notes and illustrates (1929, fig. 7), is intermediate in character between rhachitomous and embolomerous types. Well developed neural spines are present throughout the length of the tail. They are strongly inclined backward. They were obviously flattened, and even far posteriorly are seen to be square-tipped at their distal ends where well preserved. There is some suggestion that at the tip of the tail the two arches are not fused into a single spine, but in the condition of the material this is not certain. Little can be made out regarding zygapophyses or the transverse processes which one would expect on proximal caudals.

The arch bases are massive, triangular structures, their ventral apices extending far down toward the bottom of the column. Their anterior and posterior margins are, where the surface can be clearly seen, raised ridges — the anterior margins more prominently defined — and the intervening areas somewhat concave.

The intercentra, as said above, are mirror-images of the arch bases, triangular in shape as seen in side view, with dorsal apices extending up toward the top of the central region, and with bases occupying nearly the whole length of each segment ventrally. Although nowhere is an intercentrum seen in end view, it is, as noted by Watson, improbable that a complete intercentral ring was present. Intercentra of this general type were already present in rhipidistian crossopterygians, were retained in most temnospondyls, and would be expected to be present likewise in ancestral anthracosaurians. Firmly fused with the intercentra are haemal arches which, like the neural spines, slant strongly backward. The most anterior ones are incompletely preserved, but a haemal spine appears to be present on the vertebra which I interpret as caudal two, and spines continue throughout the caudal series. Anterior ones are massively built; beyond, however, they become shorter and more slender, and in the last third of the tail are reduced to rounded swellings below the intercentra.

Most interesting of vertebral elements are the pleurocentra. When seen laterally in articulated position, the pleurocentrum is a long slender band curving diagonally downward and forward between the arch base and the intercentrum of the succeeding segment. In several instances in the tail the pleurocentra are seen somewhat out of position in the form of slender half-rings. Watson suggested that the presence of these fractional rings was

due to breakage, and that in life each pair of half-rings formed
a single unit, completely surrounding the notochord. However,
the fact that a similar condition is also seen in several instances
in the presacral column (not prepared at the time of Watson's
study) strongly suggests that this "broken" condition is a
natural one, and that in life the pleurocentrum, although com-
pletely surrounding the notochord, ossified not as a single element
but as two slender hemi-cylinders. This is a condition which
might be reasonably expected as an early stage in the develop-
ment of an anthracosaurian column from a primitive protorhachi-
tomous one, and is seen as an ontogenetic stage in the disco-
sauriscid seymouriamorphs (Špinar, 1952, pp. 118-119, figs. 6-8).

Posterior trunk vertebrae. A series of vertebrae on the slab
containing the posterior half of the trunk and the hind limbs is
well exposed in ventral view. Unfortunately, however, the neural
arches are nowhere completely preserved, and the neural spines
are not visible. The intercentra are large structures, comparable
to those of typical rhachitomes, 10-11 mm wide at the ventral
midline and tapering gradually toward their upper ends. An-
terior and posterior margins are raised rims; toward the upper
ends, the narrowed lateral surface is a concave channel between
the two rims. There is a rounded longitudinal ridge at the
ventral midline, with a shallow pocket on each side and above
each pocket a secondary longitudinal ridge. The intercentra are
thin shells, and there was obviously a large persistent notochord.
Little is seen of the upper termini of the intercentra. In some
there is an indication of a notch in the posterior border, dorsally,
for rib attachment. It was earlier believed that *Pholidogaster*
was embolomerous in structure. This is not the case, for not
only are the intercentra incomplete rings, but also there are no
formed true centra. Instead, there are paired pleurocentra. In
no instance are they here seen in place; they are displaced in
various fashions, so that, fortunately, their structure can be
readily made out. Each pleurocentral element, thin externo-
internally and narrow anteroposteriorly, is curved so as to form
an arc which in life came close, it would seem, to 180°; un-
doubtedly in the trunk, as can be seen clearly in the tail, the
two pleurocentra came close to joining one another dorsally and
ventrally. In several instances the lower end as preserved is
relatively broad, the upper end slender and pointed. Presuma-
bly the lower end reached the ventral midline between successive
intercentra. The upper end slanted forward along the back

margin of its proper intercentrum and narrowed to allow room
for the pedicel of the arch, which may have been developed
somewhat as in the tail, although certainly not reaching as far
ventrally.

A number of ribs are preserved. The "lumbar" ribs are
straight, slender and short, typical lumbars having lengths of
about 15 mm, and one farther forward (about the tenth pre-
sacral) reaching a length of 37 mm. The last precaudal inter-
centrum preserved lies close to the midlength of the left femur;
it is a somewhat stouter element than those preceding it. On the
left side its posterior margin is strongly notched near its upper
end. Projecting from this notch is a stout, truncate structure
which is suggestive of a sacral rib-head; close beside it, and
partially concealed by adjacent materials, is a leaf-shaped struc-
ture which may well be the blade of a sacral rib.

Anterior trunk vertebrae. Remains of the "thoracic" region
are visible along the "lower" margin of the first postcranial
block, but were completely obscured by the dermal armor prior
to development in 1960. Preparation here proved, however, very
difficult. Attempts at acid preparation were fruitless; the dermal
scales were closely apposed to the underlying bones and it was
(and is) difficult here to tell the two materials from one another
and both from matrix, and this region of the column is un-
satisfactory. Nine intercentra, seen in ventral view, can be
identified: they are, however, incompletely exposed and, an-
teriorly, somewhat disarticulated. Swellings in the scale areas
covering the block suggest the presence of concealed intercentra
at the points marked by stars on Figure 1 A. Pleurocentra are
poorly preserved. It is, of course, impossible to determine ac-
curately the total number of presacral vertebrae; but if the head
has retained its connection with the column, the presacrals may
be estimated at thirty-six — a reasonable number for a primitive
labyrinthodont.

A number of ribs are seen at the lower margin of the block.
None is complete. They are obviously longer and broader than
the "lumbar" ribs seen on the block following posteriorly. The
heads are expanded, although the nature of the articular surfaces
is uncertain, and there are indications of expansion in breadth
distally. One rib is preserved for a length of about 40 mm, and
is obviously far from complete. No neural arches can be seen
in this series.

Pectoral girdle and limb. The clavicles are exposed on their

ventral surfaces.[1] They are broadly expanded ventrally, with an essentially triangular shape and with a typical labyrinthodont sculptural pattern of radiating ridges. The left clavicle is complete; the right is missing a fraction of its posterior margin. Poor remains of the sharply upturned ascending process are present on both sides. The anterior part of the interclavicle is present; it is seen between the two clavicles and a short distance back of them. The posterior part is absent, but a smooth impression, probably giving nearly the complete outline, is present on the matrix. A sculpture pattern is seen over the ventral surface of the interclavicle where visible, except posterior to the (incomplete) right clavicle, where a smooth surface for apposition with that bone is seen. The margins of this smooth area indicate that in life the two clavicles were somewhat more broadly separated posteriorly than as preserved, the right clavicle having been pushed somewhat medially and anteriorly. A slender rod seen at the margin of the slab close to the left clavicle can be reasonably interpreted, as Watson suggested, as the stem of a cleithrum. It would seem that the girdle was, in all probability, fairly comparable to that seen, for example, in *Archeria*. Between cleithrum and interclavicular impression are obscure remains obviously belonging to the left scapulocoracoid. A larger mass of broken material which presumably represents the right scapulocoracoid is seen at the (true) right-hand margin of the interclavicular impression and dorsal to the posterior end of that impression.

There are no preserved remains of the left front limb (the slab does not include the area where its remains would be expected). An impression on the matrix adjacent to the presumed remains of the right scapulocoracoid indicates the position of part of the upper end of the right humerus, but the middle portion of the bone lay in the position of the crack separating the slab containing the head from that containing the anterior end of the trunk. On this second slab are preserved the lower end of the humerus and incomplete radius and ulna; there are no traces of carpus or foot. The situation suggests a humeral length of somewhat under 5 cm; the lower end is 24 mm broad. The bone is seen from the ventral surface. There is a well developed entepicondyle, and an ectepicondylar surface separated

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[1] A comparable isolated clavicle from Gilmerton is present in the Museum of Practical Geology (no. axvii/1-5B).

from the under side of the entepicondylar region by a longitudinal ridge. The bone, as seen in end view, is considerably thickened above this point. There is no ossified ventral articular area for the radius, but there may have been in life a modest cartilaginous extension here. No entepicondylar foramen is seen, but the bone is somewhat crushed in the area where this might be expected.

The upper part of the ulna is preserved, and the distal part is represented by an impression. The olecranon was obviously unossified; the shaft was 22 mm long, the upper end 5 mm wide; the bone becomes more slender distally and the radial margin is somewhat concave. Much of the radius is present, but the lower part is incomplete, crushed and obscure. The upper articular surface has a width of 7 mm; the length appears to have been about 24 mm.

Pelvic girdle and limb. As Watson notes, considerable information can be obtained regarding the pelvic girdle and limb. There is no trace of the right half of the girdle, but the left half is present, its outer surface exposed, and the ilium directed ''downward'' toward the lower edge of the slab. There is the long posteriorly-directed process of the ilium common to many very primitive tetrapods (further development shows it to be broader than in Watson's figure). The region in which one would expect a dorsal iliac process for articulation with a sacral rib is damaged. Most of the outline of the acetabulum is preserved; the ischium is nearly complete; the pubis represented only by an impression.

Both femora are present, the right running forward morphologically beneath the column, the left turned upward; the left femur is seen in ventral view, the right from an anterodorsal aspect. The right femur as preserved is 46 mm in length, the left 51 mm. The width of the head is about 12 mm, the distal width the same, the slender shaft 5 mm in minimum breadth. The dorsal surface of the head, seen on the right femur, has the common pattern of primitive tetrapods: well-rounded in transverse section, and somewhat convex in outline proximally, the mid-point of the curve somewhat anterior to the line of the shaft. The exposed anterior aspect of the left femur shows the presence of a pronounced internal trochanter, with a distinct longitudinal depression developed along the anterior surface between the trochanter and the shaft proper. Unfortunately, the head region is imperfectly preserved, and little can be said except that there appears to be the usual ventral intertrochanteric fossa, bounded anteriorly by the internal trochanter. Distally,

typical anterior and posterior condylar regions are readily dis-
tinguishable on both femora, the posterior, as always, more
prominent. The two condyles are separated dorsally, as generally,
by a distinct longitudinal hollow. Ventrally, broad articular
faces for the tibia are seen, facing outward and downward at
about a 45° angle; the right femur shows that the end of the
posterior condyle was (as frequently in labyrinthodonts) un-
ossified. The anterior articular surface extends some distance
up the shaft. Ventrally a deeply excavated popliteal space is
seen, on the right femur, between the two condyles. A low but
sharp adductor crest runs proximally up the shaft from the
posterior margin of the popliteal space. Presumably it connected
proximally with the internal trochanter, but preservation prox-
imally is not good. On the whole, the femur is of a generalized
and primitive type of the sort seen, for example, in the *Pap-
posaurus* femur from the somewhat later Loanhead No. 2 Iron-
stone (Watson, 1914) or in *Archeria*.

The right tibia and fibula are seen from the anterior (extensor)
aspect. The tibia has a length of 24 mm; the head, somewhat
convex in outline, is 7 mm broad; the shaft contracts to a width
of 4 mm, then expands distally, where the width of the bone
(partially covered by a metatarsal) appears to have been 9 mm.
The fibula (as Watson notes) is, as in primitive tetrapods gen-
erally, a longer and broader bone than the tibia, with a length
of the right element of 28 mm, and widths of head (partially
covered), shaft, and distal extremity of 8, 5 and 11 mm, re-
spectively. As in labyrinthodonts generally, the distal articular
surface curves broadly proximally toward its tibial margin,
affording contact, presumably, with a proximal centrale as well
as an intermedium. On the left side the tibia is not preserved;
the element present is the fibula. Its length (as is that of its
mate) is 28 mm. It appears thin because seen from its medial
aspect. Distally the medial portion of the articular surface is
exposed.

As Watson notes, the tarsal region is difficult of determination.
The left tarsus has been exposed since his studies. Preserved
(partly as impressions) are a large proximal element and three
more distally, above the heads of the metatarsals. Possibly these
may represent an intermedium and fibulare, fourth centrale and
tibiale; but if so, we must assume that the distal tarsals and more
distant centralia have been displaced and were possibly un-
ossified. On the right side is a large element which (again) I
tend to identify as an intermedium, and several smaller and

rather obscure elements. On either foot three articulated metatarsals are present. This count is surely due to accidents of preservation, and not improbably the animal was pentadactyl. The three left metatarsals have lengths as preserved (counting from the fibular margin) of 10, 9 and 8 mm (the second and third reach the edge of a fracture in the block and may have been slightly longer). Those of the left side (counting in the same direction) have lengths of 11, 11 and 12 mm. On the left foot a further, incomplete metatarsal is present alongside the distal end of the fibula. Both feet appear to be seen from the ventral aspect. The metatarsals are essentially flat and featureless, but there is a suggestion of a slight dorsal arching of the bones along their lengths. The most medial toe of the right foot originally had three phalanges, with lengths, as seen in Watson's drawing,[1] of about 5, 2+ and 1 mm. This toe has been partially removed, to exhibit a proximal phalanx of a second toe, 7 mm long. Beyond this, Watson's figure indicates, there was formerly a second phalanx, about 4 mm in length, and a small terminal element.

Abdominal armor. The ventral armor is well preserved over most of the region between pectoral and pelvic girdles; its general disposition may be seen in Huxley's figure 1. As typically, the rows of gastralia on either side meet at a sharp angle in the midline. This midline can be traced from a point just proximal to the entepicondyle of the right humerus back, roughly parallel to the vertebral column, to a termination anterior to the head of the right femur. Along the anterior part of the trunk the midline lies but 10-16 mm to the right of the exposed vertebral centra; in the "lumbar" region, however, the midline arches to the left, to an extreme of 40 mm from the column, before curving back toward the pelvis. The squamation of the left side curved downward over the vertebrae and ribs. This area was partly destroyed during preparation of the column. The squamation of the right side, however, is fully exposed as far as it was preserved in the specimen when collected. Along the anterior part of the column the squamation extends outward but 20-30 mm from the midline, giving the diagonally-directed scale-lines a length of 25-38 mm. It is probable that the narrowness of the squamate area preserved here is due to post-mortem loss. At the middle of the back, breadth of the scale-covered area increases, and extends out some 50 mm to the far edge of the slab,

[1] The reduction is closer to × ¾ than to the × ⅔ given in Watson's legend.

giving a maximum length of scale rows, as preserved, of about
70 mm. More posteriorly, the width of the scaled area decreases
to about 20-25 mm a few centimeters in front of the pelvis; as
preserved, however, the scale rows here slant very strongly back-
ward (perhaps due to post-mortem distortion) so that their
lengths approach 50 mm.

The general pattern of arrangement of the gastralia is seen
in Huxley's figure 4. However, his illustration is rather more
than "of the natural size," for in general the scales are but
about 10-15 mm long. They are essentially oat-shaped, with
greatest widths about one-third the length. Their apparent
width is less; posterior to a longitudinal ridge, the surface of
each scale is overlapped by its neighbor, so that the average ex-
posed width is little over 2 mm. As Huxley shows (but generally
to a somewhat greater degree) the ends of the scales overlap
their neighbors in the same scale row. The maximum number of
scales in a given diagonal row does not appear to exceed ten
or so, even in the broadest preserved area of squamation. The
central element in each row is roughly U-shaped, with the two
arms of the U diverging posteriorly from one another at about
60°; anteriorly, each median scale sends forward from its
rounded central area a tongue-shaped process which underlaps
its anterior neighbors.

Skull. The skull has been crushed flat in such fashion that
the jaws were pushed somewhat to the right, the skull to the
left. A limited amount of the dermal roof is visible on the
under surface (Fig. 2). At the "lower" margin is seen a frag-
ment containing most of the left jugal. Its posterior end is
represented only by an impression, and hence its relation to
the quadratojugal is not clear. The ossification center is close
to the anterior end of the part preserved. Near the anterior
end of the jugal are fragmentary remains of the lower margin
of the left maxilla; a few small teeth are visible. The lower
margins of both premaxillae are visible. The teeth are for the
most part absent, but nearly the whole length (of about 7 mm)
of a large tooth is preserved, and there are obscure remains of
several other teeth and alveoli. Lying near the right clavicle
is the displaced right quadrate, and a broken strip of bone
anterior to it may be the right quadratojugal.

The dorsal surface of the skull was embedded in a mass of
ironstone. At my request Mr. Rixon cleaned, with considerable
difficulty, the anterior portion of this surface, revealing a series
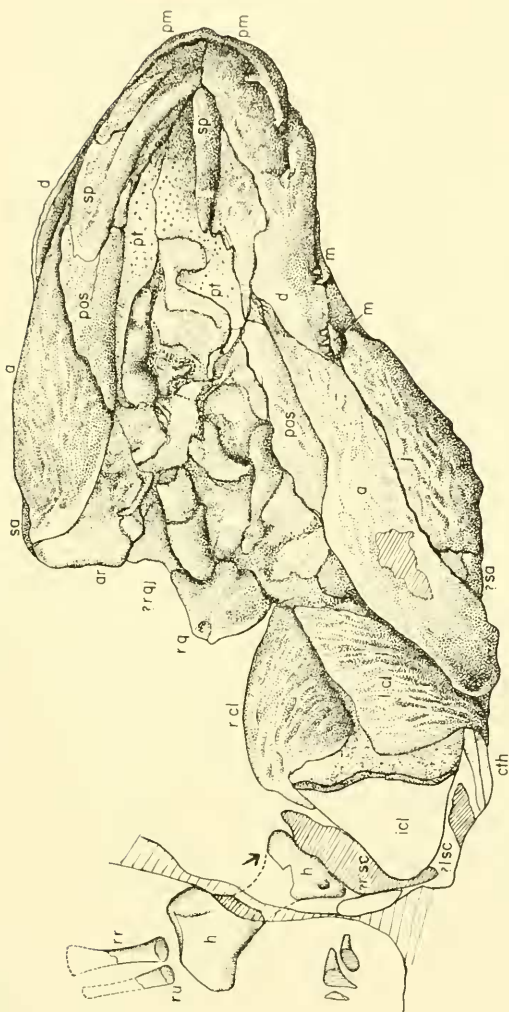of crushed and displaced fragments. A further area cleaned, in

Figure 2. Cranial and shoulder region of the type, in ventral view. × ½. *Abbreviations:* a, angular; *ar*, articular; *cth*, cleithrum; *d*, dentary; *h*, humerus; *icl*, interclavicle; *j*, jugal; *l cl*, left clavicle; *l sc*, left scapulocoracoid; *m*, maxilla; *pm*, premaxilla; *pos*, postsplenial; *pt*, pterygoid; *r cl*, right clavicle; *rq*, right quadrate; *r qj*, right quadratojugal; *r r*, right radius; *r sc*, right scapulocoracoid; *r u*, right ulna; *sa*, surangular; *sp*, splenial.

the left posterior region of the roof, exposed a mass of crushed
bone fragments impossible of interpretation, and no attempt was
made to clean the rest of the roof, since it is highly improbable
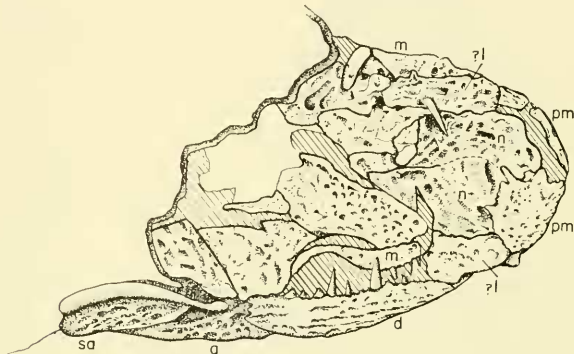that the results would be worth the effort. Anteriorly (Fig. 3),

Figure 3. Dorsal view of anterior part of head of type. $\times$ ½. *Abbrevia-
tions*: *a*, angular; *d*, dentary; *l*, lacrimal; *m*, maxilla; *n*, nasal; *pm*, pre-
maxilla; *sa*, surangular.

the right premaxilla is apparently present in toto, and a portion
of the left is seen as well. Posterior to them are good-sized
sculpture plates representing much of the nasals, and to the left
of the left nasal much of the left lacrimal and part of the left
maxilla are preserved. A fragment posterolateral to the right
premaxilla may be an incomplete right lacrimal; a tooth-bearing
strip of maxilla is seen posterior to this. I cannot be sure of the
nature of any of the more posterior skull roof fragments. The
acid preparation has preserved the sculpture pattern in excel-
lent style. There is little evidence of radial arrangement of the
ornament, which consists essentially of subcircular pits sur-
rounded by well-raised ridges.

A considerable amount of bony material, presumably pertain-
ing to the palate and braincase, can be seen on the ventral surface
between the jaws, but little of it is interpretable. Paralleling
the right jaw ramus is a long strip of denticulate bone which is
presumably part of the right pterygoid, and opposite this a
second dentate area presumably belonging to the left pterygoid.

Lower jaw. Nearly the entire external surface of both lower
jaws is exposed on the ventral aspect of the cranial slab. The
left jaw as preserved measures 186 mm from symphysis to end

of articular; one gains strongly the impression that anterior and
posterior portions have been pulled somewhat apart. The right
jaw appears much shorter, measuring 140 mm in length as pre-
served, due to the fact that it was so broken post-mortem that
the posterior portion has pushed forward under the anterior
part. Very probably the actual length in life was on the order
of 160 to 170 mm. In the left ramus the distortion is such that
the splenial elements, which curved medially toward the ventral
surface in life, are flattened into the plane of the angular and
dentary, thus giving an impression of greater than true depth.
Several fragments include most of the dentary, but nowhere
is its alveolar margin present. The left surangular is nearly
completely covered by a plate including most of the jugal. Over
much of the posterior part of the angular region the surface is
eroded. On the dorsal side (not figured) the articular surface
is nearly completely visible; it is, as in many primitive forms,
divided into two areas which are at nearly right angles to one
another and separated by a rounded ridge. Anteromedially,
there is here seen a ridge representing the posterior end of the
prearticular and, below this, the thickened rounded ventro-
medial margin of the angular.

On the right side, as noted above, anterior and posterior seg-
ments of the broken jaw over-ride one another. The anterior
segment includes splenial, postsplenial and part of the dentary.
The dentary is so broken that much of its posterior portion is
turned over to appear on the upper surface of the slab. Here
the middle portion of the tooth row is present, although poorly
preserved. Of the posterior segment, the greater part of the
angular is seen on the lower aspect. At the back, crushing is
such that the articular is seen in posterior view, but preserva-
tion is poor. Dorsally is seen a small portion of the angular
and the overturned upper portion of the surangular, including
its curved upper margin; much of the extent of this bone appears
to have been lost from the margin of the slab.

Our knowledge of the lower jaws of the type is, thus, confined
almost entirely to the outer surface. The pattern obviously
conforms to that common to many primitive or generalized
labyrinthodonts, and shows no diagnostic character of any sort.

The Edinburgh skull and jaws. Watson (1929) identified as
probably belonging to *Pholidogaster* a skull in the Royal Scottish
Museum (no. 150.561) which, from the character of its matrix,
appears to come from the Gilmerton ironstone. I see no reason
to dissent from this identification. The size and shape are

appropriate. I have estimated the jaw length in the type as about
160-170 mm; the length of a jaw associated with this Edinburgh
skull is 163 mm. As can be seen, the skull is diagnostically
anthracosaurian, as would be expected from the "subanthraco-
saurian" nature of the vertebral column. The sculpture of the
skull roof is more sharply defined in the type skull, but this is
attributable to the acid preparation of the type, whereas the
Edinburgh specimen is a split block, in which sculptured ridges
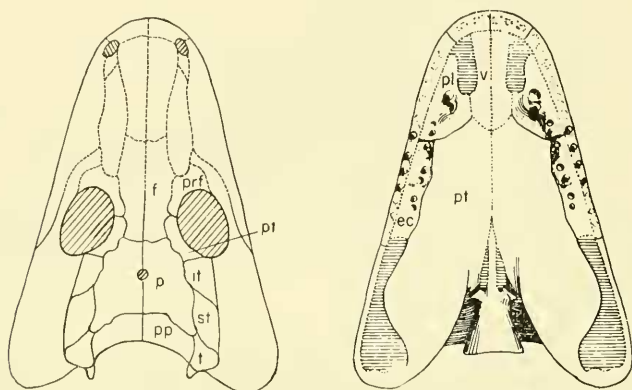are seldom sharply preserved.

Figure 4. Dorsal and ventral views of the Edinburgh skull, modified from
the restoration by Watson. *Abbreviations: ec,* ectopterygoid; *f,* frontal;
it, intertemporal; *p,* parietal; *pf,* postfrontal; *pl,* palatine; *pp,* postparietal;
prf, prefrontal; *pt,* pterygoid; *st,* supratemporal; *t,* tabular; *v,* vomer.

I reproduce (Fig. 4) Watson's attempted restoration of this
skull, with some additions resulting from restudy of the specimen.
The skull table is comparable to that of embolomeres, particularly
in the fact that, as in that group, the well developed intertemporal
extends forward to nearly completely separate postfrontal and
postorbital. I believe the tabular-postparietal suture can be
made out on the right side in approximately the position indi-
cated by Watson. The outer margins of the supratemporal and
tabulars curve downward toward the plane of the cheek, but
the fact that the right cheek has broken off from the table
along the plane of suture between squamosal and table indicates
the presence of the zone of weakness here expected in anthra-
cosaurians. On the right side of the facial region there are

indications of part of the sutural pattern, and I have indicated
sutures here (with doubt) as broken lines. It seems probable
that the lacrimal was excluded from the orbital rim by a pre-
frontal-jugal contact. There is a break parallel to the tooth row
which Watson has interpreted as the upper border of the maxilla.
I rather think, however, that this break lies along the length
of the lateral line groove, and that anteriorly the maxilla ex-
tended farther dorsally. I can make no more of the palatal
aspect than the features shown in Watson's reconstruction.

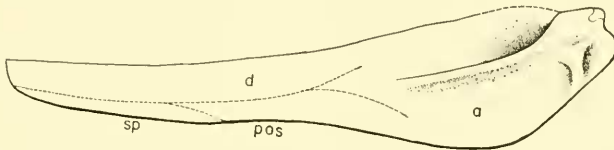The right lower jaw (Fig. 5) is completely preserved as to

Figure 5. Inner view of the right mandible of the Edinburgh specimen.
Anteriorly, the inner surface is absent, so that indications of sutures of
elements of outer surface are seen. × ½. *Abbreviations:* *a,* angular; *d,*
dentary; *pos,* postsplenial; *sp,* splenial.

length, but crushed and partially covered by the skull. It is
slender anteriorly, gradually deepening posteriorly. Little can
be made out regarding the external surface except that anteriorly,
where the inner surface of the jaw is missing, there can be seen
indications of sutures between the dentary and a narrow splenial
and, more posteriorly, a second splenial element. The inner
surface is preserved posteriorly. There is a strong medial proc-
ess extending inward below the articular region, apparently
corresponding to the region seen in ventral view as part of the
crushed right jaw of the type. The inner face of the jaw below
and anterior to the articular region is deep; its upper margin,
forming the inner rim of the adductor fossa, bears a low but
definite ridge. Farther forward, little can be made out of the
inner jaw aspect, but enough is present to show that the large
fossae in this region which are characteristic of embolomeres
were not present.

Lower jaw teeth are not seen, but maxillary teeth are pres-
ent. As in the type they are numerous, small and slender; when
completely preserved they are seen to be slightly recurved at
their tips, and there is some indication of striation in the basal

part of the teeth. They are spaced 3.5 to 4 mm apart. It would appear that replacement was actively underway at the time of death, with empty alveoli between most of the teeth present. There is no indication of a developed canine region, but such teeth as are well preserved suggest a region of maximum length of about 10 mm at a point somewhat anterior to the midpoint of the maxilla. Presumably the tooth row (including empty alveoli) included (as Watson's figure suggests) about 30 teeth.

DISCUSSION

Restoration. Because of the unique nature of this skeleton, I have thought it worth while to attempt a restoration — this despite our inadequate knowledge of certain features (Pl. 1, B). Uncertainties regarding skull structure have been noted earlier. The endochondral shoulder girdle and cleithrum are incompletely known, but it is reasonable to restore these elements according to the common pattern found in forms removed as far from one another as the embolomere *Archeria* and the rhachitome *Eryops.* The manus is missing, the ribs are incompletely known, and few data are available regarding presacral neural arches, but we cannot go far wrong in restoring absent elements in the fashion common to most labyrinthodonts. With his short limbs, long trunk and well developed tail, *Pholidogaster* was, obviously, primarily a water-dwelling form as, presumably, were all primitive labyrinthodonts.

Phylogenetic position of Pholidogaster. In many regards *Pholidogaster* is a rather generalized and essentially primitive labyrinthodont. The specimen is well ossified and obviously mature. With a length of about 117 cm — less than four feet— it is a much smaller animal than such well known Carboniferous labyrinthodonts as the large embolomeres of the *Pteroplax-Eogyrinus* group and such a large loxommid as *Megalocephalus.* On the other hand, it is not far from the size of the ancient ichthyostegids, and labyrinthodonts with proportions similar to those of *Pholidogaster* occur at various later levels of the Carboniferous.

Apart from the vertebral centra, the postcranial skeleton shows few diagnostic features. The broadly triangular clavicular plates are presumably primitive in character. Such plates are characteristic of embolomeres and seymouriamorphs in later times, but broad clavicular plates are present in some seemingly primitive temnospondyls (as well as advanced forms) and are seen in the

archaic ichthyostegids. The interclavicle is unfortunately incomplete; it was obviously long, but elongation is found in some temnospondyls as well as in anthracosaurs, and one cannot tell whether or not the long stem essentially diagnostic of the later group was present. The ilium shows a long posterior process plus, apparently, the small ascending blade for sacral rib articulation. This structure has long been recognized as one found in the embolomeres and such further anthracosaurians or seymouriamorphs as *Diplovertebron* and *Discosauriscus*. But since we now know that this type of ilium was already developed in ichthyostegids, this feature, again, is not a diagnostic one. Too little is known of limbs in early labyrinthodonts to make profitable an attempt at diagnosis on the basis of limb bones.

The vertebral structure, however, is almost unique. As described above, the intercentra are the prominent elements of the central region — massive structures, although incomplete dorsally, which form the main supports of the neural arches. The pleurocentra have the form of paired half-rings, surrounding the notochord; they are slender but extend the full depth of the central region.

It is entirely reasonable to assume that the vertebral structure of *Pholidogaster* represents an initial stage in the development of the anthracosaurian vertebral column, leading to the structures present in embolomeres, seymouriamorphs and typical reptiles.

Because of the prominence of the embolomeres in collections of Carboniferous amphibian materials, it was at one time assumed that this type of vertebral structure was a basic one for labyrinthodonts; that there had been derived from this, on the one hand, the rhachitomous and stereospondylous types, in which pleurocentra became reduced and the intercentrum became dominant, and, on the other hand, a series in which the ring-shaped embolomerous intercentrum was progressively reduced, thus leading to seymouriamorphs and reptiles.

It has, however, become apparent in recent decades that the embolomeres were far from being the sole labyrinthodonts in the Carboniferous. It now seems clear that, despite their retention of a number of primitive features, the embolomeres are merely a subgroup of one of the two major lines of labyrinthodont evolution — the Anthracosauria; a parallel radiation of rhachitomous forms was also taking place during the Carboniferous.

As a result, I proposed in 1947 an alternative scheme of labyrinthodont evolution — one in which the ancestral type possessed vertebrae which were not embolomerous but proto-rhachitomous

(Fig. 6). Typical crossopterygians, from which labyrinthodonts may be reasonably derived, have in many instances large wedge-shaped intercentra and very small paired pleurocentra, situated dorsally near the lower margins of the neural arch. To develop from this the temnospondylous type of vertebra seen in the Rhachitomi requires no change except some modest increase in the size of the pleurocentra to strengthen the column by filling
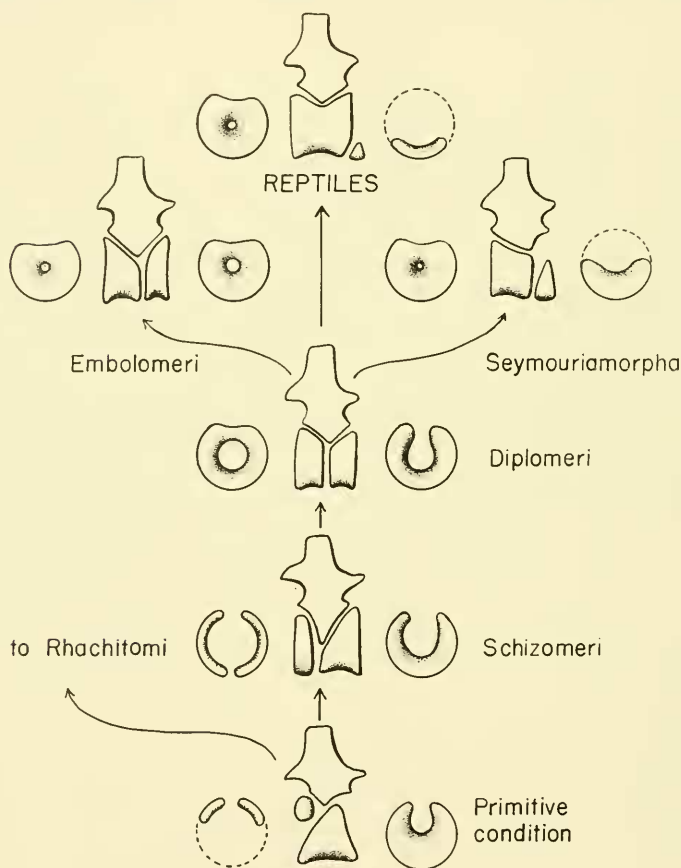

Figure 6. Suggested evolutionary series of anthracosaurians, with a typical vertebra representing each stage or group. In each case the vertebra as a whole is seen from the right side; at the left the pleurocentra (or centrum) shown in end view; at the right, the intercentrum in end view.

out the gaps in the dorsal part of the central region where ossi-
fication had been lacking. To develop an anthracosaurian type of
vertebra would demand a major development of the pleurocentra.
They should expand and coalesce to form a ring-shaped true
centrum. Beyond this stage, completion of a ring-shaped struc-
ture of the intercentrum as well would lead to the embolomerous
condition as a side line; on the other hand, reduction of the
intercentrum would lead to the conditions seen in seymouria-
morphs and typical reptiles.

Support for this theory of vertebral evolution was given by
Jarvik's description (1952) of the vertebral column of ichthy-
ostegids. In them, as in many crossopterygians, the pleurocentra
are very small, dorsally placed, paired elements. To be sure, the
ichthyostegids are probably somewhat off the main line of laby-
rinthodont evolution, but the presence here of proto-rhachitomous
vertebrae is strongly suggestive of the general scheme of vertebral
evolution which I had advocated.

Further support of this theory is afforded by the vertebral
condition of *Pholidogaster*. If we are to form a true centrum
from the small, dorsally placed pleurocentra of an ancestral
crossopterygian, downward growth, toward the bottom of the
column, of these paired elements is the first change to be expected
— this to be followed later by a fusion of the two pleurocentra
into a complete, true central, ring. This theoretically expected
stage is perfectly exemplified in the two half-rings of the
Pholidogaster centrum. The assumption that this condition is
phylogenetically antecedent to the formation of a true centrum
is reinforced by the ontogenetic condition described by Špinar
(1952, pp. 118-119, figs. 6-8) in the seymouriamorphan family
Discosauriscidae. Here the larger specimens show a complete
true centrum; but smaller and more immature individuals show
paired hemicylinders corresponding closely to those of the mature
Pholidogaster. In the older individuals the two hemicylinders
fuse ventrally and, still later, dorsally, to complete the mature
central structure.

Although the attribution of the Edinburgh skull to *Pholido-
gaster* is not capable of absolute proof, the phylogenetic impli-
cations of the structures seen in this skull are in perfect harmony
with those derived from vertebral structure. The proto-anthra-
cosaurian build of the *Pholidogaster* vertebrae call for the pres-
ence of a skull with anthracosaurian attributes; the definitely
anthracosaurian nature of the Edinburgh skull calls for a

vertebral column of anthracosaurian or proto-anthracosaurian build.

That the Edinburgh skull is anthracosaurian cannot well be doubted. The tabular "horns" are of modest size, and are not, as Panchen and Walker (1960) have pointed out, of the long, pointed embolomere type; such structures are quite surely specializations of the embolomeres, and not to be expected in generalized anthracosaur ancestors of seymouriamorphs and typical reptiles as well as embolomeres. Four diagnostic features may be expected in the skull of an ancestral anthracosaurian: (1) A tabular of good size which, as emphasized by Säve-Söderbergh (1935) and Steen (1938), articulates with the parietal — this in contrast to the reduced tabular of temnospondyls. Such a tabular is present in *Pholidogaster*. (2) A loose attachment of cheek to skull table with, posteriorly, a wedge-shaped otic notch. Current (and reasonable) belief as first advocated by Watson (1926) is that this is a primitive situation, retained from the fish stage; later anthracosaurians leading to seymouriamorphs and typical reptiles have modified this structure, but it is characteristically retained in embolomeres. In theory, the ancestral temnospondyl may have had this structure as well, but fusion of cheek and table and development of a rounded rather than a wedge-shaped otic notch obviously occurred at an early stage in temnospondyl evolution. The Edinburgh skull is primitive in construction, but the Gilmerton deposits are fairly well up in the Lower Carboniferous, and the time element speaks strongly for the Anthracosauria here. (3) In rhachitomes, postfrontal and postorbital are broadly connected back of the orbit, and the intertemporal, when present, is widely separated from the orbital rim. In embolomeres, in strong contrast, the intertemporal pushes toward the orbit so that there postfrontal and postorbital barely touch one another. In reptiles the intertemporal is normally absent and in seymouriamorphs it is reduced, so that a fair area of postfrontal-postorbital contact is developed. But the contact is still narrow in many seymouriamorphs and the embolomere condition may be reasonably regarded as primitive for anthracosaurians. The *Pholidogaster* intertemporal is emphatically of the type of the presumed anthracosaurian ancestor. (4) In all typical rhachitomes, including the loxommids (and in the ichthyostegids as well), the muzzle is broadly rounded and on the palatal aspect the nares are widely separated, with between them broad platelike vomers bearing a prominent tusk-pair. In embolomeres, in

contrast, the nares are close together in the narrow snout, separated only by narrow strap-shaped vomers which lack tusks. Primitive reptiles show this same condition, which can hence be reasonably regarded as primitive for anthracosaurians. This pattern is present in the Edinburgh skull, further reinforcing belief as to its pertinence to the Anthracosauria. Too great reliance, however, should not be placed on this last feature, for it is obviously correlated in considerable measure with snout shape, and seymouriamorphs with broadly rounded muzzles approximate the rhachitome condition.

In sum — the vertebral construction of the type and diagnostic features found in the Edinburgh skull indicate that in this Gilmerton amphibian we are dealing with a primitive member of the anthracosaurian group of labyrinthodonts.

Labyrinthodont classification. In 1947 I reviewed the Labyrinthodontia at some length, and established a classification based on all evidence then available. A major cleavage was made into two groups: Temnospondyli (including typical rhachitomes and stereospondyls, the loxommoids and ichthyostegids)and Anthracosauria (including the embolomeres and forms leading to reptiles, with the semouriamorphs dangling, so to speak, on the amphibian-reptilian boundary). This dichotomy was based to some degree upon cranial characters of the sort discussed above, but primarily on divergence in vertebral structure — continued emphasis on the intercentrum among the temnospondyls, in contrast to a strong trend among anthracosaurs toward development of a typical centrum from the tiny paired pleurocentra of ancestral forms.

Various advances made during the decade and a half since this essay at classification suggest that reappraisal of the situation may be in order. The basic concept of a division into temnospondyls and anthracosaurians appears to have been reinforced by later discoveries, including the presence of proto-rhachitomous vertebrae in the ichthyostegids, as noted above, and of rhachitomous vertebrae in the previously doubtful loxommids (Baird, 1957).

Perhaps the one advisable major change would be the separation of the Ichthyostegalia as a third, minor but distinct, labyrinthodont group. To be sure, my inference that their vertebrae were rhachitomous has been validated, and they agree with the temnospondyls rather than anthracosaurians in fusion of cheek and braincase, a rounded otic notch, and broad vomers. But even Jarvik's preliminary descriptions show such a series

of primitive characters that it is difficult to associate the ichthyo-
stegalians closely with the more advanced temnospondyls of later
times. Further, currently accepted tenets assume that the inter-
temporal was part of the ancestral skull pattern of labyrintho-
donts; its absence in the ichthyostegids suggests that they were,
even at this early stage, somewhat of a side line. Accordingly,
it is perhaps preferable to consider the ichthyostegal forms as
a third, distinct group of labyrinthodonts, as follows:

> Superorder (or Subclass) Labyrinthodontia
> > Order (or Superorder) Iehthyostegalia
> > Order (or Superorder) Temnospondyli
> > Order (or Superorder) Anthracosauria

I shall refrain here from discussion of the temnospondyls,
although work being done at present, by Baird and Carroll, for
example, suggests progress toward sorting out true phyletic lines
among the Rhachitomi in preference to the somewhat artificial
grouping which I used in my 1947 classification. With regard
to the ichthyostegalians, it is possible that with further knowledge
the East Greenland forms will prove to be but one, possibly aber-
rant, subgroup of an archaic group which will also include forms
more directly ancestral to later temnospondyls and anthraco-
saurians.[1] It is pleasant to find that my suggestion (put forth
in 1945) that *Otocratia* is related to the ichthyostegids is sup-
ported by the finding of a comparable otic construction in an
East Greenland genus (Jarvik, 1952). However, my further
suggestion that the colosteids of the Pennsylvanian are much
evolved ichthyostegids has not gained support either from new
materials or from the opinions of my colleagues.

Our present concerns are with the anthracosaurians (Fig. 6).
As I pointed out in 1947, the major evolutionary event in early
anthracosaurian history must have been the development of a
complete ring-shaped centrum from the primitive, small, paired,
pleurocentral elements, the intercentrum remaining persistently
large. Once the true centrum evolved, further evolution could
have proceeded in two directions — on the one hand, to the
embolomeres with development of a ring-shaped intercentrum,
and, on the other, to seymouriamorphs and typical reptiles with
reduction of the intercentrum. In *Pholidogaster* we have a
half-way stage in the development of a centrum, with the ring

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[1] I am sometimes tempted to speculate that the ichthyostegid skull pattern may
be related to the peculiar arrangement seen in microsaurs, but there is, of course,
not the slightest positive evidence for such a belief.

completed spatially, but consisting of two discrete, pleurocentral halves. At the moment there is no other typical anthracosaurian known to me which has such a structure as an adult, although rather surely *Pholidogaster* had predecessors, contemporaries and possibly successors exhibiting this structural stage. As noted earlier, Špinar (1952, fig. 6, etc.) figures specimens of *Discosauriscus* (*Discosaurus*) in which the centrum is in the form of two "pleurocentral" half-rings, and Credner (1893) also figures this condition. However, as Špinar clearly demonstrates, we are here dealing with larval forms; the adult was a seymouriamorph, in which there was a complete central ring.

Despite the lack of known relatives, it seems reasonable to consider *Pholidogaster* as representative of a stage in anthracosaurian evolution which may be reasonably termed the suborder (or order) Schizomeri — the name referring to the "broken" appearance of the pleurocentral ring.

Vertebrae with a construction of this same sort are described by Eaton and Stewart (1960) in *Hesperoherpeton*, a tiny amphibian from the Pennsylvanian of Kansas. They consider this form as the type of a new order, the Plesiopoda. I hesitate, however, to use this term for the stage in anthracosaurian evolution represented by *Pholidogaster*. The skull of *Hesperoherpeton*, as described by Eaton and Stewart, departs wildly not only from that of the anthracosaurians but from that of any known labyrinthodonts; the pectoral limb is equally aberrant and seemingly primitive and fish-like, and the ordinal term has reference to foot structure, not to vertebral type. Possibly *Hesperoherpeton* is a larva whose metamorphosed adult would have had a more normal labyrinthodont structure; again, this form may represent an aberrant side branch from the schizomeran stage of anthracosaur evolution; still again, it may represent an independent group developed from ancestral forms in parallel fashion to the anthracosaurs as regards vertebral structure.

Next above the schizomeran level should be one in which the two pleurocentra should have fused to form a complete ring centrum, but in which there persisted an intercentrum incomplete dorsally, but still retaining full height from the bottom level of the column to an articulation with the neural arch. Certainly, considering the radiation in the later Carboniferous of embolomeres, seymouriamorphs and true reptiles which developed from forms in this structural stage, animals of this sort must have evolved before the close of the Mississippian.

There are, however, few described specimens which appear to
fall in this category. Somewhat comparable vertebrae from the
Upper Carboniferous Joggins tree stumps of Nova Scotia
occur on a slab containing a fragmentary skull described
by Steen as *Dendryazousa* (Steen, 1934, fig. 17). As described,
however, this skull fragment is not of an anthracosaurian type,
but in this material, juxtaposition is no guarantee of association,
and the vertebrae might perhaps belong to the anthracosaurian
termed *Calligenethlon* (Steen, 1934, pp. 484-486, figs. 18, 19,
20 B, pl. 2, fig. 1). To add to the confusion, it is quite possible
that these animals trapped in hollow stumps may be immature
and hence incompletely ossified; a ''grown-up'' *Calligenethlon*,
for example, may have been a true embolomere. On somewhat
safer grounds may be the materials described from the Pennsyl-
vanian of Nýřany by Fritsch (1889, pp. 11-13, pls. 50, 52, 53;
cf. Steen, 1938, p. 239) as *Diplovertebron*[1] (although even here
possible conditions of immaturity cannot be ruled out). In
Diplovertebron the vertebrae, as seen in side view, appear to be
those of an embolomere, with both intercentrum and true cen-
trum parallel-sided structures extending full height to the neu-
ral arch base. In end view, however, the intercentrum is incom-
plete dorsally; the embolomere condition is not attained.

This stage, albeit imperfectly known at present, seems clearly
defined and should be named. A name derived directly from
Diplovertebron might be confusing (as well as lengthy); Diplo-
meri (by analogy with Embolomeri) may be utilized as a
subordinal term for this stage, with *Diplovertebron* used, provi-
sionally, as a type genus until a more ancient, more truly
ancestral type be described.

Unless the evolution of a ring centrum occurred more than
once, in parallel fashion, among early anthracosaurs, the Diplo-
meri were a group from which not merely embolomeres but
seymouriamorphs and typical reptiles have been derived.[2] The
pattern of evolution beyond the diplomerous stage may have
been complex. Whether or not the Seymouriamorpha are to be
considered reptiles or amphibians remains a moot point. In
this group the Discosauriscidae, as Špinar (1952) has shown,

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[1] Drs. James and Margaret Brough inform me that certain materials sometimes
assigned to this genus (as well as those of *Solenodonsaurus*) are properly to be
assigned to *Gephyrostegos*.

[2] I hope to return at a later date, after a description of the cranial structure of
the microsaur *Pantylus*, to a discussion (*contra*) of the hypothesis that part, at
least, of the reptiles were derived from lepospondyls.

have a gilled larva ; but it is not impossible that amniote patterns
of development may have already been present in the early
embryonic stages of such a form. In the partially reduced inter-
centra, the Seymouriamorpha show a stage of vertebral evolution
to be expected in reptile ancestors ; but the broadly-developed
otic notch of typical seymouriamorphs shows a development
hardly to be expected in reptilian ancestors. Possibly we have,
in such animals as *Gephyrostegos*, a line paralleling the sey-
mouriamorphs and leading more directly to later reptile groups.
I trust that work on Pennsylvanian faunas undertaken by Drs.
James and Margaret Brough and others will shed light on this
important area. It is, however, beyond the proper limits of the
present discussion. I shall at the moment follow this classifica-
tion :

Order (or Superorder) Anthracosauria

Suborder (or Order) Schizomeri. Centrum formed
of two discrete half-rings ; intercentrum very large,
but not complete dorsally. Typical incised otic
notch, cheek loosely articulated with skull table.
No coracoid ossification. Ilium primitive, as in
embolomeres.

Suborder (or Order) Diplomeri. Centrum a complete
ring ; intercentrum large, but not complete dorsally.
Otic notch primitive. No coracoid ossification. Ilium
as in embolomeres.

Suborder (or Order) Embolomeri. Both centrum and
intercentrum complete rings. Otic notch primitive.
No coracoid ossification. Ilium persistently primi-
tive.

?Suborder (or Order) Seymouriamorpha. Centrum
complete, but ossified intercentrum, while persist-
ently large, not extending upward to neural arch.
Cheek and table fused, otic notch highly developed.
Ascending and posterior processes of ilium joined
to form an iliac blade. Separate coracoid ossifica-
tion.

In the discussion above I have made no mention of amphibian
groups, recent or fossil, other than the Labyrinthodontia. It
has generally been considered that the Anura are related in
some fashion to the Labyrinthodontia, and Watson (1940) advo-
cated descent from *Amphibamus* of the Pennsylvanian, a form
obviously related to the rhachitomes. It was on this account that

I erected, in 1947, a subclass Apsidospondyli to include labyrinthodonts and frogs. Subsequent work by Gregory (1950) appears to show that *Amphibamus* is actually a rhachitome, but the possibility of this does not exclude a rhachitomous origin for the Anura. In a recent paper, however, Parsons and Williams (1963) point out various features possessed in common by frogs and urodeles and suggest a common origin for the two groups. If this proves to be the case, the labyrinthodonts will have no descendants except the reptiles, and the term Apsidospondyli is perhaps redundant.

Although I fail to be convinced by Jarvik's arguments for a separate origin of urodeles from fishes (Romer, 1962; cf. Thomson, 1962), the fact that we find throughout the Carboniferous and early Permian varied series of small, non-labyrinthodont amphibians, which I have classed as lepospondyls in a broad use of that term, presents an evolutionary problem for which we have at present no solution. As Watson (1929) notes, amphibians of this sort, already highly specialized, are present in the Lower Carboniferous, at a far earlier age than any labyrinthodonts except the ichthyostegalians. Neither in their spool-shaped holospondylous vertebrae nor in known skull structures do they show the slightest indication of relationship to Labyrinthodontia. It is hoped that restudy of the oldest, Scottish, types will yield further light on their structure. But even so, we will still be confronted here with a major problem in early tetrapod evolution.

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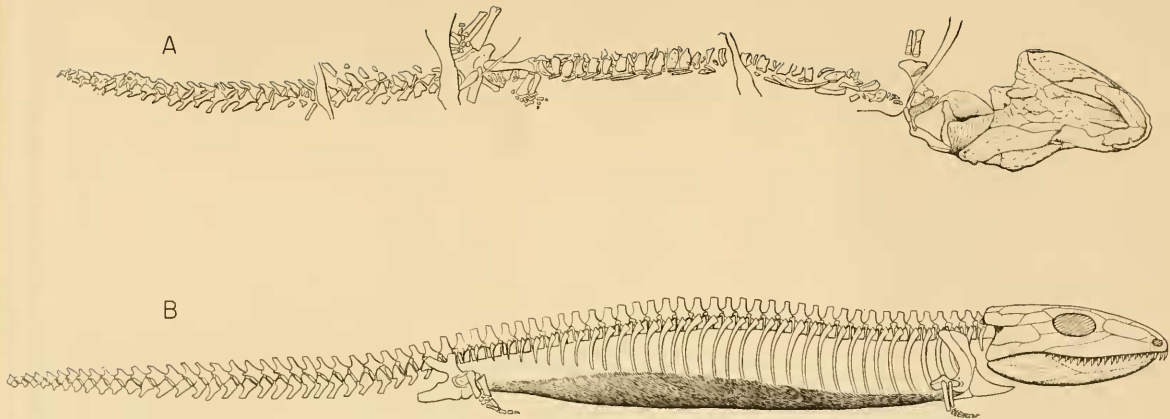
Plate I. *A*, the type specimen of *Pholidogaster pisciformis*, × ¼. Squamation omitted. *B*, attempted restoration, × ¼. As noted in the text, dorsal neural spines, scapula and manus are unknown, and the ribs are incompletely preserved.